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Estimation of annual production of Testacea (Protozoa) in mull and moder (II)[1])

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With 6 figures

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1. Introduction

The present study deals with the results of investigations on the production of Testacea in mull soils. Earlier investigations reported the production of Testacea in moder (Schönborn 1975, 1978). In the literature there are several articles on the associations of Testacea in different forms of humus (e.g. Bonnet 1964; Bonnet & Thomas 1960; Bamforth 1968, 1971; Bunescu 1971; Coûteaux 1972; Korganova 1975; Lousier 1975; Rosa 1957, 1961; Schönborn 1973; Stout 1968). It is therefore possible for the first time to make comparisons on the production of Testacea in mull and moder and their parameters. Investigations on the decomposition of empty shells in mull and moder were also made.

2. Site and methods

2.1. The soil

Investigations were made from December 1979 to November 1980 in a deciduous forest near Jena (GDR, Thuringia). The vegetation consists of ash *(Fraxinus excelsior)*, *Acer platanoides*, *Aesculus hippocastaneum*, coppiced *Cornus sanguinea* and a ground flora dominated by *Aegopodium podagraria*.

The humus type is mull: C/N 21.8; *p*H (H_2O) 7.0.

The geological subsoil consists of shell lime. The thickness of humus averaged 0.5 cm (1 m² soil contained ~5 liters of humus).

Indicators (Testacea): *Centropyxis plagiostoma*, *Plagiopyxis minuta; Paraquadrula discoides*. A few indicators of moder also exist.

2.2. The estimation of production and its parameters

The production of Testacea were estimated as described by Schönborn 1975, 1978. Production chambers (length 7 mm, diameter 3 mm) were sealed by two membrane filters (10 μm pores).

The soil volume of the chambers averaged 0.01 ml. This relatively small volume of soil is sufficient for the development of exposed Testacea. The decomposition of empty shells was rapid, that's why the chambers were exposed only 2—3 days. Therefore it is desireable to use a very small soil volume for exposure.

In order to recognize living animals in invisible shells, it was necessary to stain with phenolic aniline blue. The formula of production (P) is: $P = S_t + s_t - (S_p + s_p)$.

Where S_t = number of full shells in the chamber after time t; s_t = number of empty shells in the chamber after time t; S_p = number of full shells in the parallel sample at the beginning of the time of exposure; s_p = number of empty shells in the parallel sample at the beginning of the time of exposure.

Biomass (B), number of generations and mortality were calculated as described by Schönborn (1975, 1978).

To determine the generation times a few individuals (i) were placed in extra chambers and examined every 3 days (d) up to the moment of cell division. The number of soil exposures for this investigations amounted to 5—8 distributed throughout the year.

1) Contribution to the VIth International Congress on Protozoology, Warszawa, Poland (1981).

2.3. The measure of decomposition of empty shells

A sample of humus, which contained Testacea, was first dried in the air (+20 °C), and later in an oven (6 hours at a temperature of +40 °C and 15 minutes of +100 °C). After this treatment all individuals were dead and their shells undamaged. Suspensions were made from the samples. The suspension water was obtained by the filtration of untreated diluted samples. In this way, a normal microflora for decomposition was preserved. The empty shells were numbered in the chambers for exposure in the soil. The control interval was 3 days. The investigations were made n mull and moder during moist weather in April, 1980.

3. Results

3.1. The annual production

The annual production amounted to ~26 g biomass/$m^2 \cdot a \triangleq 940 \cdot 10^6$ i/$m^2 \triangleq 1.3$ g $C_{org}/m^2 \triangleq 50$ kJ (Table 1). The calculation of production values in square meters refer to a humus layer thickness of 0.5 cm. The adjacent mineral horizon was not colonized by Testacea. *Trinema lineare*, *Trinema enchelys* and *Microchlamys patella* were the dominant species in the production of individuals and *Centropyxis plagiostoma*, *Centropyxis aërophila* var. *sphagnicola*, *Euglypha ciliata*, *Trinema enchelys* and *Microchlamys patella* were dominant species in the production of biomass. *Trinema enchelys* and *Trinema lineare* have a highest density and *Centropyxis plagiostoma*, *Centropyxis aërophila* var. *sphagnicola* and *Trinema enchelys* had the highest biomass in the annual average. *Trinema enchelys* was a key-species in the turnover of the Testacea association. Strikingly small was its P/B. This is also true for the most other species. On the average the P/B amounted to 44. In only a few species did the P/B value exceed 100 *(Microchlamys, Corythion)*. The possible reasons for the relatively small P/B will be discussed later.

3.2. Daily production, mortality, number of generations and generation times

The highest value of daily production was found among individuals of *Trinema lineare* in September 1980: 16 i/0.01 ml soil · d (min: 1.3 i/0.01 ml in December, average value, when the species is present: 4.7 i/0.01 ml). *Plagiopyxis minuta* had the smallest daily production: 0.12 i/0.01 ml. In the soil of the study site the species was not rare, but in the chambers the cell division was recorded only two times. Table 2 lists the daily production of Testacea during chosen time periods. These data show that there was no relationship between abundance and production.

Table 3 includes the values of mortality, number of generations and generation times. The mortality was relatively high. In almost one-half of the species studied the mortality was recorded at more than 10 %/d. The average value in moder and water was between 5 and 6 %/d. *Phryganella acropodia* showed a strikingly small mortality together with a long generation time. Foissner & Adam (1981) also found the longest generation time in *Phryganella*. The same was true for *Plagiopyxis minuta*. There appeared to be a connection between a high mortality and a short generation time. However the present investigation doesn't show a clear picture of this relationship. The number of annual generations was relatively small. It was significently higher in moder than in mull (Schönborn 1975).

3.3. The relationship between abundance, production and mortality

The annual curves of abundance of four choosen species are shown on Fig. 1 and Fig. 2. These animals represent two related lobose *(Centropyxis)* and two related filose *(Trinema)* species. Within both species-couples one species was dominant, the other less abundant. The less abundant species in their occurrence join the annual curve of the dominant species. There was no principle of exclusion. In spring the abundance curve oscillated; whereas it stabilized from summer to winter. This trend can also be seen on the curve of total abundance (Fig. 3). Generally, the abundance curves turned out differently in relationship to seasons (Couteaûx 1975, 1976).

Table 1. Annual sums and averages of data for the calculation of Testacea production in a mull soil

Species	$\bar{x}$ i/0.01 ml	$\bar{x}$ i/m² (×10⁶)	Σ P/0.01 ml (i)	Σ P/m² (i×10⁶)	$\bar{x}$ B/m² (mg)	Σ P/m² (mg)	P/B (a)
Microchlamys patella	2.8	1.4	289.0	144.5	22.3	2,297.5	103.0
Centropyxis aërophila	0.6	0.3	4.2	2.1	17.1	120.1	7.0
C. aë. var. *sphagnicola*	10.0	5.0	144.2	72.1	252.0	3,634.0	14.4
C. plagiostoma	3.0	1.5	99.2	49.6	302.8	10,000.0	33.0
C. orbicularis	0.1	0.05	7.6	3.8	8.9	674.5	75.8
Cyclopyxis kahli	0.3	0.1	5.5	2.7	8.0	216.5	27.1
Plagiopyxis minuta	0.9	0.4	11.2	5.6	18.0	252.6	14.0
Paraquadrula discoides	0.1	0.05	2.8	1.4	0.7	21.0	30.0
Phryganella acropodia	5.1	2.5	110.4	55.2	51.0	1,126.0	22.1
Euglypha ciliata	2.2	1.1	63.0	31.5	112.2	3,213.0	28.6
E. rotunda	3.5	1.7	130.0	65.0	12.4	474.5	38.2
Tracheleuglypha acolla	3.4	1.7	29.8	14.9	32.8	287.6	8.8
Assulina muscorum	0.6	0.3	57.0	28.5	1.3	128.2	98.6
Trinema enchelys	13.2	6.6	221.6	110.8	139.3	2,337.9	16.8
T. lineare	13.2	6.6	531.0	265.5	17.1	690.3	40.3
T. complanatum	7.7	3.8	65.9	32.9	36.5	315.8	8.6
Corythion dubium	0.8	0.4	86.4	43.2	0.8	82.1	102.6
C. pulchellum	0.2	0.1	22.2	11.1	0.2	24.4	122.0
Σ, $\bar{x}$	**67.7**	**33.6**	**1,881.0**	**940**	**1,033.4**	**25,896** ≙ **50 kJ**	**43,9**

Annotation: dry weight = 11 % of live weight (KALMUS 1931), 17,5 J/mg dry weight (ROBERTSON 1979).

Table 2. Daily production of Testacea in choosed times in a mull soil

Time	p	a
23. 1./11. 2.	6.6	44.4
11. 2./26. 2.	0.4	12.2
1. 4./10. 4.	10.4	288.5
6. 5./13. 5.	0.0	95.1
1. 7./16. 7.	20.0	62.4
16. 10./20. 10.	12.3	28.5
18. 12./27. 12.	4.0	9.8

Note: p = Daily mean production (i/0.01 ml · d), a = Density at the beginning of the time of exposure (i/0.01 ml).

Table 3. Mean mortality in days ($\overline{M/d}$), number of generations per year (G/a) and mean duration of generation in days ($\overline{T}$) of Testacea in a mull

Species	$\overline{M/d}$ (%)	G/a	$\overline{T}$ (in days)
Microchlamys patella	14.2	18	2.3
Centropyxis aërophila var. *sphagnicola*	12.5	7	2.0
C. plagiostoma	4.8	14	4.3
Plagiopyxis minuta	0.0	2	8.0
Phryganella acropodia	1.8	14	4.2
Euglypha rotunda	9.7	12	2.8
Trinema enchelys	15.2	15	2.0
T. lineare	11.4	22	2.0
T. complanatum	7.1	9	1.8

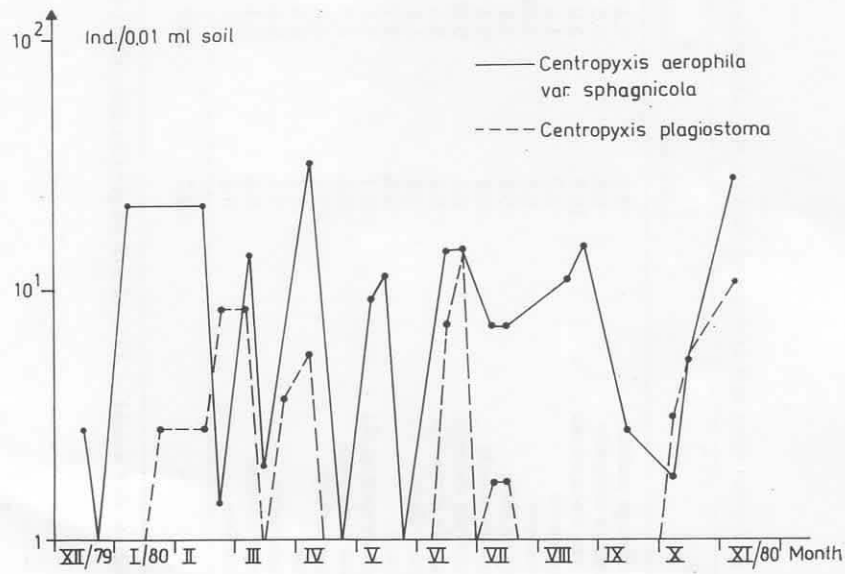

Fig. 1. Seasonal distribution of *Centropyxis aërophila* var. *sphagnicola* and *Centropyxis plagiostoma* in mull.

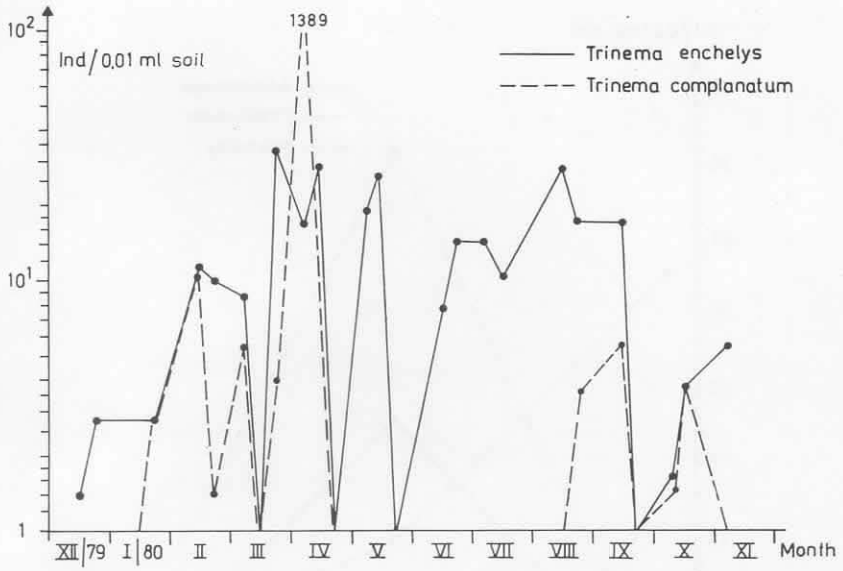

Fig. 2. Seasonal distribution of *Trinema enchelys* and *Trinema complanatum* in mull.

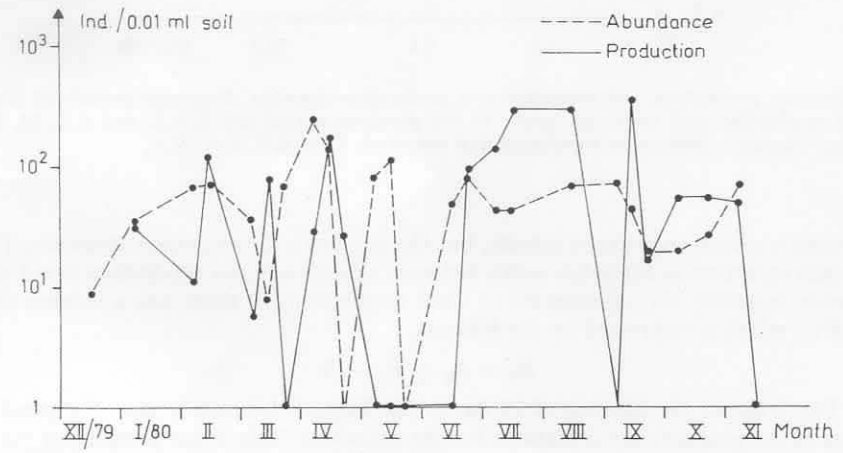

Fig. 3. Density and production of Testacea in mull. The production values apply to the time, which in each case is the last point marked. Because of the short exposure (2—3 days), each value represents a sum of various measures of production. The scale of time (abscissa) is schematic. The distance between two marks within a month amounted to nearly 7—8 days.

In Fig. 3 the abundance curve is compared with the curve of production. A relation between abundance and production which was already mentioned will not be elaborated. In previous experiments where slides were exposed in a river there was a relationship between abundance and production of Testacea. With increasing of density the number of cell divisions decreased. The production was at zero. The high abundance was maintained because of the long life of individuals (Schönborn 1981). It was not determined wether a similar relationship in soil-inhabiting Testacea exists, or whether the use of experimental chambers affected this relationship.

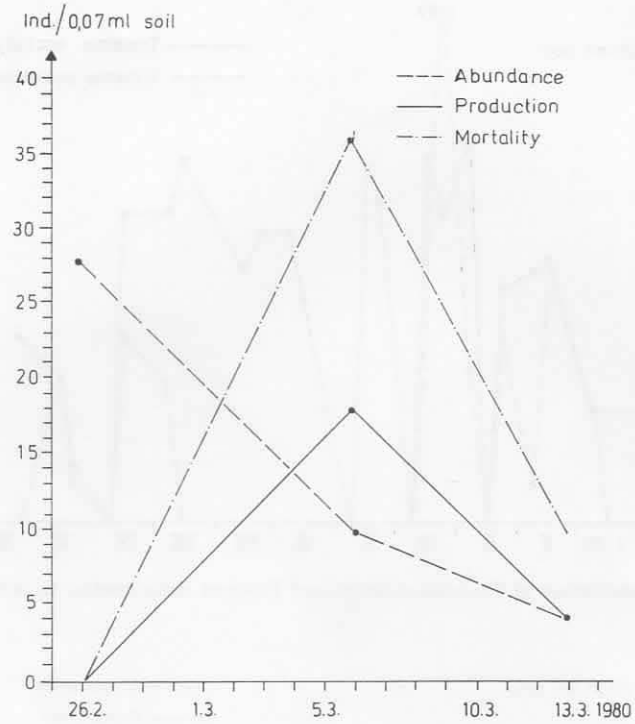

Fig. 4. Density, production and mortality in a production-chamber. Exposure-period: 16 days. The values of production and mortality apply to the previous period (26. 2./6. 3. and 6. 3./13. 3.). The empty and damaged shells were numbered and removed: 1. 3., 6. 3. and 10. 3.

The slide is a homogeneous substrate, but the soil has a heterogenous structure. The role of substrate structure in the relationship between abundance and production is not clear.

Between mortality (M), abundance (A) and production (P) there was a balance (SCHÖNBORN 1981), which is expressed by the formula

$$M_t = A_0 + P_t - A_t$$

The Fig. 4 shows the balance of 16 days. The balance formula is also the proof of the exactness of the production calculations for the chambers. This is not possible, of one works with parallel samples, as in the present case. It's an approximate calculation.

The values in Fig. 4 were obtained by exposing supplemental chambers in the soil. Only species with transparent shells were used. The exact values of the test are:

26. 2.—6. 3.	6. 3.—13. 3.
$M_t = 36$	$M_t = 10$
$A_0 = 28$	$A_0 = 10$
$P_t = 18$	$P_t = 4$
$A_t = 10$	$A_t = 4$

3.4. Biomass and cell size

The biomass was calculated by the help of the cell volume (Table 4). In comparison with biomass of the moder inhabiting individuals, there are significant differences (SCHÖNBORN 1975, 1978).

Table 4. Mean weight (mg) expressed as 10^6 individuals

	mg wet wt
Microchlamys patella (Claparède et Lachmann)	15.9
Centropyxis aërophila Deflandre	57.2
Centropyxis aërophila var. *sphagnicola* Deflandre	50.4
Centropyxis plagiostoma Bonnet et Thomas	201.9
Centropyxis orbicularis Deflandre	177.5
Cyclopyxis kahli Deflandre	80.2
Plagiopyxis minuta Bonnet	45.1
Paraquadrula discoides (Penard)	15.0
Phryganella acropodia (Hertwig et Lesser)	20.4
Euglypha ciliata (Ehrenberg)	102.0
Euglypha rotunda Wailes et Penard	7.3
Tracheleuglypha acolla Bonnet et Thomas	19.3
Assulina muscorum Greeff	4.5
Trinema enchelys (Ehrenberg)	21.1
Trinema lineare Penard	2.6
Trinema complanatum Penard	9.6
Corythion dubium Taranek	1.9
Corythion pulchellum Penard	2.2

Note: Number of measured individuals/species = 10.

Generally, individuals, which live in moder as well as in mull, have a greater size in mull than in moder. The biomass of species living in mull was higher than species in moder (Table 5). The measurements were made on 130 individuals representing 13 species. *Trinema enchelys* showed 2 sizes, one with normal shells and the other with big shells. The form with normal shells had twice the abundance of those with big shells. The average length of the normal form was 43 μm (min.: 33.0 μm; max.: 52.8 μm), and the length of the big form amounted to 78.2 μm (min.: 69.3 μm; max.: 92.4 μm). This phenomenon was already noticed by Laminger (1978). In a subalpine meadow the increase of shell size was correlated with an increase in soil moisture. This phenomenon is supposed to be widely distributed. Mull soils are moister than moder.

This circumstance may explain the increase of biomass in mull. Laminger reported measurements of both forms at 30 μm and 80 μm, which correspond to my values.

It's interesting, that *Centropyxis aërophila* appears in two sizes too. The average length of the normal form was 52.8 μm, and that of the big shells 72.6 μm. Transition forms seldom occurred.

3.5. Decomposition of the empty shells

The decomposition of the shells in mull was very rapid. After 2 days 8 % of the shells were decomposed and after 6 days 50 %. That means, the exposure should last not longer than 2—3 days. The total decomposition of the empty shells lasted ~27 days.

In moder the decomposition was essentially slower. After 14 days ~7 % of the shells were decomposed and after 28 days 50 %. The time of exposure of production chambers in moder should not exceeds 14 days. The decomposition of all shells well be attained within 85 days (Fig. 5).

Differences of the decomposition time between Euglyphidae-shells (idiosoms) and Centropyxidae-shells (xenosoms) could not be stated.

In raw humus the decomposition of shells is supposed to be still slower than in moder. The time of decomposition explains the different density of empty shells in the forms of humus. The decomposition takes place in morphological perceptible stages (Fig. 6).

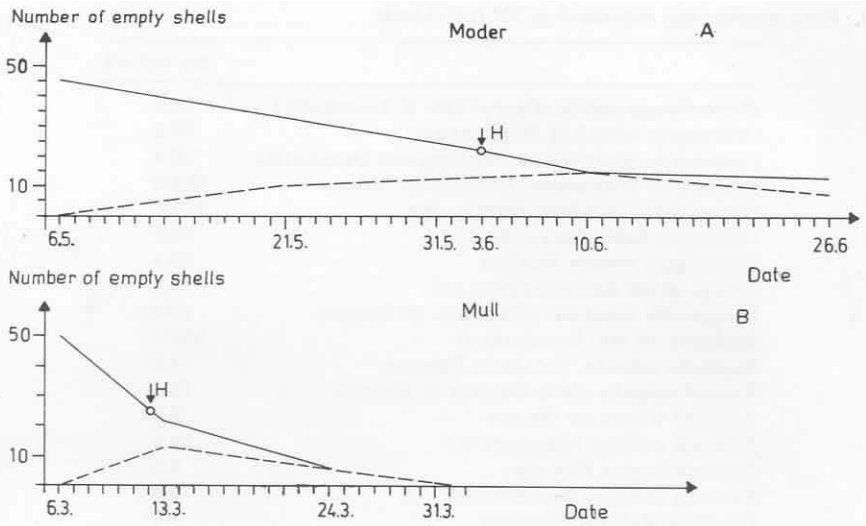

Fig. 5. Decomposition of empty shells in moder and mull. Number of intact empty shells (———); Number of damaged shells (-------); Half-time of decomposition (H).

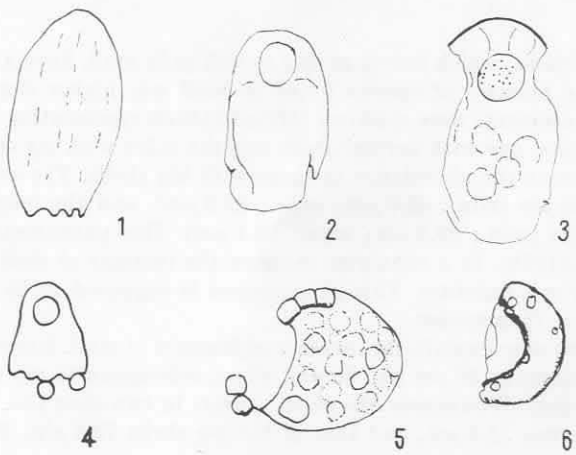

Fig. 6. Morphological decomposition stages of Testacea-shells in soils. (1) *Euglypha ciliata* (1. phase). (2) *Trinema galeata* (2. phase). (3.) *Trinema complanatum* (2. phase). (4) *Trinema enchelys* (3. phase, scales come out). (5) *Centropyxis orbicularis* (2. phase). (6) *Cyclopyxis kahli* (3. phase).

Phase 1: The scales of Euglyphidae-shells are invisible. The little stones of the Centropyxidae-shells partially fall down.

Phase 2: The flanks of Euglyphidae-shells pull down; from the Centropyxidae-shells parts break out.

Phase 3: The shells break into in pieces. By drying the shells can also "wave" and pull down.

3.6. Comparison of the Testacea production and its parameter in mull and moder

A comparison between the various coenotical characteristics of the Testacea-associations is rendered more difficult by the limited data; nevertheless I would like to make this com-

Table 5. Comparison of the coenotical characteristics of Testacea associations in mull and moder

	Mull	Moder
Production (i/0.01 ml · a)	1,881	503
Production (mg/m² · a; 5 l soil)	25,896	3,144
P/B	44	110
Mean generation time (in days)	3.3	3.0
Mean mortality (%) / d	8.5 (dom. species > 10 %)	6.5 (total species > 10 %)
Mean number of generations / a	12.5	28.0
Density (random tests: May 1972; i/ml)	180	247
Empty shells (random tests: May 1972 shells/ml)	516	2,287
Biomass (Euglyphidae) (mg/m²; 5 l soil)	353	13.5
Biovolume of species ($\bar{x}$ mm³/10⁶ i)	46.3	36.0

Note: Summarized and calculated after values by SCHÖNBORN 1973, 1975, 1978, and present data.

parison because it goes beyond the special problems of Testacea research and gives general references on the biological processes in both forms of humus. Table 5 gives a survey of the measured data. The data indicate a lesser density of full and empty shells in mull than in moder (most of the cited literature also confirms this). Production and mortality, however, were higher in mull. The decomposition of shells takes place four times faster in mull than in moder. The production of biomass was eight times greater and that of individuals four times higher in mull than in moder. Recently, MEISTERFELD (1980) recorded in a meadow-mull soil a higher density of full shells than in forests-moder soils. It's remarkable, that the P/B (and in the same time the turnover) was lower in mull than in moder. This phenomenon needs a special explanation. In mull the cell size and biomass of the species are bigger than in moder. High biomass and high production show a smaller P/B than a lower biomass and high production. A high biomass reduces the P/B.

In moder the biomass was much smaller than in mull. Thus, a high P/B does not always attain the production found in mull. In mull the average generation time lasts longer than in moder. In spite of this there was a higher production of individuals in mull than in moder. The reasons are not so clear than by the high biomass production.

The production of individuals was essentially due to 3 species: *Microchlamys patella*, *Trinema enchelys* and *Trinema lineare*. Their production amounted to 55.5 % of total production. *Microchlamys* has a P/B of 103, while the species of *Trinema* show a high average density. These characteristics in the course of the year cause the high individual-production of the association.

The number of annual generations in mull was lower than in moder. This is amazing, indeed, because the density in mull fluctuates less than in moder. It can be supposed, that the reasons for this is that there is less exposed volume of soil. This was very distingtly demonstrated by *Plagiopyxis minuta* which divided only two times in the chambers. This can partially explain the small P/B on "effect of chamber".

A general concept of biomass of Testacea in soils has not been made. HEAL (1965) recorded values of 2 g/m² in antarctic soils, while SUDZUKI (1979) found only 3 mg/m² in Japanese soils. However, all parameters of production must be brought into relationship to population dynamics in order to interpret them. That's very difficult and requires much time. Moreover, the biomass should be considered in connection with the diversity (MEISTERFELD 1978).

4. Discussion

The Testacea production in soils is similar to production of mesofauna although sometimes it's higher. While the biomass of nematodes in mull can be 35-times higher than

that of Testacea (Volz 1951), their production is not essentially higher. Thus Wasilewska (1979) found in agricultural soils a net production of nematodes of 61.1—75.3 kJ/m² · a (data converted). [Thomas (1979) recorded a net production of Oribatei of 9—12 kJ/m² · a.]

Foissner & Adam (1981) investigated production and generation times of Testacea associations in alpine soils. The maximum production measured by them amounted half as much (1,005 mg in the monthly average) than the values which I determined in my investigation (2,158 mg/m² in the monthly average). It can be supposed that the inclement climatic conditions of the alpine region reduce the production and extended the generation times.

Laminger (1980) reported considerable fluctuations of generation times in alpine soils. The fluctuations depend on soil and season. It is possible, that in periods when the population density increases the generation times are short; whereas in periods of low density the generation times are long. An exact proof of this which was demonstrated on exposed slides in a river (Schönborn 1981), can not be given for soils at this time. According to Laminger the generation times fluctuated between 22 and 165 hours in an alpine Curvuletum and between 23 and 57 hours in a subnivale Elynetum. Lousier (1974) found generation times of soil Testacea between 7.2 and 10.9 days in a Canadian aspen woodland.

An interesting problem is how food conditions influence Testacea in mull. In raw humus and moder the Testacea particles of detritus are contained in the nutritive vacuoles; whereas they are missing in individuals examined in mull.

Laminger (1978) stated that the selection of food is probably dependent on soil moisture. In periods with low soil moisture individuals of *Trinema enchelys* eat detritus particles; howevers in moist soil they eat bacteria. In general, mull soils are more moist than moder. That's why in mull the Testacea seem to eat bacteria. This must have an influence on population dynamics and production. Thus the ingestion of bacteria can cause a higher biomass.

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Synopsis: Original scientific paper

Schönborn [Schoenborn], W., 1982. Estimation of annual production of Testacea (Protozoa) in mull and moder (II). Pedobiologia **23**, 383—393.

In a mull soil near Jena (GDR, Thuringia), the density, biomass, annual and daily production, mortality, generation time, number of generations and cell size of Testacea were investigated. The values for net production are: $940 \cdot 10^6$ individuals/m^2 a · ≙ 25.8 g biomass/m^2 · a (≙ 1.3 g C_{org}, 50 kJ), P/B = 44.

Production and mortality were estimated in special production chambers, which were exposed in the soil. The time of exposure was 2—3 days.

In the chambers there was a relationship between mortality, density and production.

Other values are: Mean production per day 0.0—20.0 i/0.01 ml soil; number of generations per year 2—22; mean mortality 0.0—15.2 %/d; generation time 1.8—8.0 days. In mull 50 % of the empty shells were decomposed after 6 days and in moder after 28 days.

In comparison with the testate amoebae in moder, the species in mull have a low density (live animals and empty shells), but a high production and mortality and a quick decomposition of shells.

The biovolume of species and the biomass in higher in mull than in moder.

Most characteristics of production and population dynamics are dependent on the kind of soil.

Key words: Testacea, Protozoa, annual production, mortality, biomass, abundance, generation time, cell size, mull, moder.